# Natural image statistics predict organization of retinal ganglion cell arrays

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Ganglion cells comprise about ~15 distinct types whose arrays each cover the retina completely and independently. Within an array, one cell's dendrites typically extend to its neighbors somas. Consequently, receptive fields overlap to a degree that merges the individual receptive fields into a flat sensitivity surface. But is this organization optimal for signaling natural scenes? Statistical regularities in natural scenes determine how spatial information is integrated optimally. The shape of individual receptive fields has been predicted by balancing the trade-off between increasing signal-to-noise ratio and reducing redundancy. We followed an analogous approach to determine the optimal spacing of the arrays.

We recorded from pairs of neighboring brisk-transient cells (guinea pig) to measure the overlap of dendritic and receptive fields. Since the ON and OFF subtypes form independent mosaics with different densities, we measured them separately. When neighboring cells were dye-injected, their dendritic fields were seen to overlap. OFF cells overlapped slightly more than ON cells. Confocal microscopy confirmed that the dendritic tips of one cell approximately reached the soma of its neighbor.

Spatial receptive fields were mapped using a random checkerboard stimulus and fit to a difference-of-Gaussians function. The mean spacing (receptive field center separation in units of $\sigma$) between ON centers was $2.0 \pm 0.6\ \sigma$, and between OFF centers it was $1.8 \pm 0.5\ \sigma$, where $\sigma$ denotes the standard deviation of the center Gaussian. The surround gain (relative to the center) averaged 0.73 (ON) and 0.80 (OFF); the surround size (relative to center) averaged 1.45 (ON) and 1.36 (OFF). In subsequent analyses, we used the average spatial filters (ON and OFF) obtained from this reverse-correlation analysis to model the array's responses to natural images.

Ganglion cells were modeled as summing directly from cones, whose output signal-to-noise ratio was determined from vesicle release rates at different light intensities, assuming Poisson vesicle release. Intensities were chosen from a standard database of natural images. Relative surround size, surround gain, and the absolute distance between cells were fixed to match physiology. For this array, increasing receptive field size had two effects: SNR increased (as more cones were summed), and redundancy increased (as receptive fields overlapped more). These two effects competed so that information in the array peaked at spacings of $1.8\ \sigma$ (ON) and $1.7\ \sigma$ (OFF), within the error of the measured values. These results were robust to variations in absolute spacing, surround gain, surround width, and cone SNR.

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